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THE MORPHOLOGY OF MONASCUS PURPUREUS.*

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BARKER's account of the morphology and development of *Monascus* in the early part of 1903,¹ as will be remembered, was shortly afterward questioned in a contradictory paper by IKENO.² IKENO gave, in fact, a diametrically opposite interpretation of certain of the more important phenomena connected with the spore formation in this fungus, and even went so far as to assert positively that BARKER's "Samsu" fungus did not belong to the genus *Monascus*. If BARKER is right, then *Monascus* shows close resemblances to other Ascomycetes; if, on the other hand, IKENO's views are correct, the fungus is an aberrant form.

The main points of difference between these opposed views may be concisely stated as follows. BARKER maintains that sexual reproduction results in the formation of ascogenous hyphae. The ascogonium consists, according to him, of an elongated penultimate cell; while the original terminal cell, which is pushed over to one side by the growth of the enlarging ascogonium, constitutes an antheridial branch. Fusion takes place between the two, the elongated tip of the female cell functioning in this act as a kind of trichogyne. After fusion, this tip portion is cut off by a septum and its protoplasmic contents, as well as that of the antheridial branch, finally become disorganized and eventually disappear. It is the cut off penultimate cell of the ascogonial branch, called by BARKER the "central cell," which still further develops and produces the ascogenous hyphae. This central cell becomes enormously swollen and is invested at maturity almost completely by a mass of closely clasping sterile hyphae. During its enlargement and development it affords protection and nutriment to the growing ascogenous hyphae. The latter

* This work was done under a grant from the Carnegie Institution.

¹ BARKER, B. T. P., The morphology and development of the ascocarp in *Monascus*. Ann. Botany 17:167-236. pls. 12-13. 1903.

² IKENO, S., Ueber die Sporenbildung und systematische stellung von *Monascus purpureus* Went. Ber. Deutsch. Bot. Gesell. 21:259-269. pl. 13. 1903.

arise, according to the evidence obtained by this author, as an outgrowth of the swelling central cell, which grows over the surface of the latter, closely applied to it, until it finally pushes in, or invaginates, the enlarged central cell. In this invaginated cavity, or little "nest," thus produced, the ascogenous hyphae are formed, whether as bud-dings of the end of the in-pushing hypha, or simply as segments of it, the author does not make clear. At any rate, growth continues until the closely entwined hyphae occupy almost the whole of the interior of the enveloping perithecium. "Asci are eventually produced from the ascogenous hyphae, and in each of them eight ascospores are produced. When the spores are ripe, the asci and ascogenous branches degenerate, the surrounding central cell having by this time lost its contents, remaining as a brown cuticularized enclosing wall. The spores are thus liberated into the cavity enclosed by this wall, and the ripe perithecium appears to be nothing more than a brown cuticularized sporangium-like structure." (*L. c.*, p. 204.)

IKENO apparently agrees with BARKER in regard to sexual reproduction in *Monascus*, although his evidence appears to be drawn from dubious sections, judging from his one drawing of the process. IKENO's main point of dispute with BARKER lies, however, in the method of spore-formation. He asserts that there are no ascogenous hyphae in the *Monascus* which he studied, but that, on the other hand, so-called "spore mother-cells" arise by free cell formation. The cytoplasm of the ascogonium becomes, according to him, aggregated about certain nuclei, resulting in the formation of uninucleate "Cytoplasmaballen," or "spore mother-cells." According to BARKER's account, these "spore mother-cells" are segments of a hypha, which become rounded up into asci. IKENO further notes that the "Cytoplasmaballen" become increased in number by fission, and that they may contain, at the culmination of nuclear division, a greater number of nuclei than is necessary for spore-formation, and he says that the extra ones degenerate. Usually six or eight spores are finally produced, which are, in his opinion, formed by free cells formation, leaving a small amount of epiplasm between and surrounding the spores, thus corresponding to conditions observed in the ascus. An agreement is noted in the final phenomena connected with the development of the fungus, in that in the mature spore fruit

the walls of the "spore mother-cells" become disorganized, thus setting free the spores within the perithecial wall. IKENO concludes with the assertion that WENT's classification of *Monascus* among the Hemiasci is strictly correct, and that BARKER's fungus is not a member of the genus *Monascus*, but that it is a typical Ascomycete.

Several important differences will be at once noted in these two accounts, the crucial difference being the one which concerns the origin of certain structures in the swollen ascogonial cell, or "central cell," as BARKER terms it. IKENO conceives of these structures, the "Cytoplasmaballen," as arising by free cell formation, simply by an aggregation of cytoplasm around certain nuclei; other nuclei in the ascogonium taking no part whatever in the process. BARKER, on the other hand, thinks that these deeply staining bodies are segments of one or more hyphae which have grown in from the outside of the central cell, and that the ultimate origin of these ascogenous hyphae is as outgrowths of the central cell itself, which finally turn and grow again into the cell from which they have sprung. Both assert that these bodies bear within them later the spores, and in other respects the two accounts in the main agree.

DANGEARD proposes now to assist us out of our difficulties by making BARKER's *Monascus* a new species. KUYPER,³ the latest writer on the subject, accepts this suggestion, and in a study of both *M. purpureus* Went and *M. Barkeri* Dang., finds confirmation in the main of IKENO's conclusions, although he calls IKENO's "spore mother-cells" true asci. He adds, however, the additional observation that a nuclear fusion precedes the development of the young asci. *Monascus Barkeri* differs, according to his views, from *M. purpureus* in an important respect. In *M. Barkeri* he has the nuclei fusing in pairs *before* the formation of the asci, and in *M. purpureus*, *after* the asci are formed. In *M. Barkeri*, his observation agrees, therefore, with BARKER's assumption that nuclear fusion in pairs occurs in the enlarging ascogonium. KUYPER regards this fusion as analogous to the fusion in the young ascus of *M. purpureus*, but such a fusion as he describes in the latter should be referred rather to the later

³ KUYPER, H. P., De peritheciumontwikkeling van *Monascus purpureus* Went en *Monascus Barkeri* Dang. Kon. Akad. van Wetenschappen, Amsterdam 13:46-294. 1 pl. 1904.

fusion which is known to occur in the young asci, whereas his fusions in *M. Barkeri* belong to the early sexual fusions, as are seen in *Pyronema* and other forms.

As BARKER and others have pointed out, the development of *Monascus* from the germination of the ascospores or the conidia up to the formation of the fructifications may be readily followed out in hanging drop cultures. Observations of living cultures of *Monascus* in hanging drops show that a fusion appears to take place between the basal cell of the antheridial branch and the tip portion of the ascogonial branch, which BARKER likens to a trichogyne. It appears likely that in some cases, at least, this fusion takes place after the cutting off of the tip of the ascogonium, although BARKER asserts that the act must take place before the wall is thrown across. The swelling up of the central cell and later an appearance which suggests the pushing in or invagination of the swollen central cell by some body which enters generally near the side on which the stalk is seen; further, the enlargement of this invaginated part until the central cell seems to be entirely displaced by it; and, finally, the appearance of vacuole-like bodies within the invaginated cavity and the final formation of spores, which adhere for a time in little groups, all may be readily traced in hanging drop cultures.

When one attempts to explain these appearances, however, by an examination of sections, one meets with many difficulties, as is evidenced by the remarkable differences obtained by the investigators above mentioned. I have seen in but few instances, in fact, a hypha-like outgrowth from the central cell, and, perhaps somewhat less rarely, the actual pushing in of a hypha-like body into the side of the central cell, thus forming the "nest," or invaginated cavity, in which the ascogenous hyphae develop. Another theory than that held by BARKER has suggested itself to the writer, which is borne out by many observations. Instead of the ascogenous hypha arising from the central cell, it may have its origin in the "trichogyne-like" end of the ascogonial branch. The following observations point to this conclusion. First, the rarity of protuberances from the central cell which are long enough to furnish absolute conviction that the outgrowth is a hyphal branch. They may as well be, as BARKER himself intimates, a bulging out of the swelling central

cell at a point where the investment formed by the covering hyphae is incomplete. Secondly, the fact that, in very thick sections, one sometimes finds that the invaginated cavity of the central cell is connected with the outside by a comparatively large, broad opening, where we might naturally expect a small, narrow one, since the ascogenous hyphae are relatively small. The large opening suggests the pushing in of a larger body, possibly the fertilized "trichogyne" cell above mentioned. Lastly, the frequency of occurrence in early stages of a comparatively large, deeply staining cell, lying to one side of the swollen central cell and not yet pressed into it, indicates that this deeply staining body is not a hypha with the origin BARKER attributes to it, but is instead the cell above mentioned. Should this prove true, then the fertilized ascogonial cell is in reality the end cell, while the enormously swollen penultimate cell performs a sort of "nurse-cell" function, ultimately becoming entirely displaced, its contents digested and absorbed, by the ascogenous hyphae developing within it.

That the structures growing within the cavity in the central cell are segments of ascogenous hyphae, I have no doubt; therein I agree perfectly with BARKER. For one may see in sections of almost every immature fructification young segments which are elongated and twisted and hypha-like, and which sometimes show evidences of dividing by fission, as is pointed out by IKENO. Later, these segments become rounded off and vacuoles appear in them; still further development results in the formation of their eight spores.

The *Monascus* species which I have used was first sent from Java some years ago by D. G. FAIRCHILD to ERWIN F. SMITH and was regarded by the latter as *M. purpureus* Went. Professor HARPER, who in turn received some material from Dr. SMITH, has turned the fungus over to me for examination. So far as I am able to judge from gross measurements, and from a careful comparison of figures, this form agrees with BARKER's description of his *Monascus*, and as well with the accounts of WENT, UYEDA, and others, so that my opinion is that IKENO and BARKER worked with similar forms. I find therefore in the main a confirmation of the conclusions of BARKER, as well as satisfactory explanations of the misinterpretations of IKENO.

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